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THE *CALAMUS JAVENSIS* (ARECACEAE: CALAMOIDEAE) COMPLEX IN HISTORICAL BIOGEOGRAPHIC CONTEXT

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ABSTRACT
ATRIA, M. & VAN WELZEN, P. C. 2021. The *Calamus javensis* (Arecaceae: Calamoideae) complex in historical biogeographic context. *Reinwardtia* 20(1): 1−7. — *Calamus javensis* is a very polymorphic species with a number of recognisable forms (of which several were once even recognized at species level). A historical biogeographic analysis showed no historical distribution pattern in the diversification of these various forms. The forms are very likely the result of adaptation to local circumstances, whereby more or less identical forms can develop under similar niche circumstances in disjunct areas, exceptions are the '*acuminatus-polyphyllus*' form and *C. tenompokensis* that are recognisable and present in a non-disjunct area.

Key words: Arecaceae, *Calamus javensis*, historical biogeography, species complex, taxonomy.

ABSTRAK
ATRIA, M. & VAN WELZEN, P. C. 2021. Jenis *Calamus javensis* (Arecaceae: Calamoideae) kompleks dalam hubungan sejarah biogeografi. *Reinwardtia* 20(1): 1−7. — *Calamus javensis* adalah jenis yang sangat polimorfik dengan sejumlah bentuk yang dapat dikenali (beberapa di antaranya telah dikenali pada tingkat jenis). Analisis sejarah biogeografi tidak menunjukkan adanya pola distribusi sejarah dalam proses diversifikasi berbagai bentuk tersebut. Bentuk-bentuk tersebut kemungkinan besar merupakan hasil adaptasi terhadap keadaan lingkungan lokal, dan bentuk-bentuk yang kurang lebih memiliki kesamaan morfologi merupakan hasil dari proses adaptasi terhadap relung ekologi yang sama di daerah yang terpisah secara geografi. Bentuk '*acuminatus-polyphyllus*' dan *C. tenompokensis* merupakan pengecualian karena mudah dikenali dan terdapat di area nondisjungsi.

Kata kunci: Arecaceae, *Calamus javensis*, jenis kompleks, sejarah biogeografi, taksonomi.

INTRODUCTION

Presently, the largest genus in the rattans, climbing palms, is *Calamus* L. (subfam. Calamoideae) with *ca*. 400 species (Henderson, 2020). Especially since phylogenetic analyses (Kramadibrata, 1992; Baker *et al.,* 2000a & 2000b) proved it to be paraphyletic with the genera *Ceratolobus* Blume ex Schult. & Schult.f., *Daemonorops* Blume, *Pogonotium* J.Dransf. and *Retispatha* J.Dransf. nested within it, which Baker (2015) synonymized with *Calamus*.

Within *Calamus*, *C. javensis* Blume is a slender, very polymorphic rattan commonly present in the everwet rainforests of southeast Asian. In the course of time many taxa have been split from it and various forms are recognizable (see names in Table 1 and Fig. 2). Most of the names have been synonymized again with *C. javensis* (Barford & Dransfield, 2013; Henderson, 2020). Within the complex only *C. tenompokensis* Furtado proved to be recognizable, in a morphometric, phenetic analysis (Atria *et al.*, 2017) as well as in a specimen level phylogenetic analysis (Atria *et al.*, 2020). This species is generally an accepted taxon (Henderson, 2020). Unfortunately, the phylogenetic analysis (Atria *et al.*, 2020), based on two markers (the chloroplast *mat*K and the nuclear 5S), gave no real satisfying resolution for most specimens in the analysis. Only the 5S marker provided some structure in the cladogram in which most branches were not supported (in Fig. 2 the highly supported groups are indicated as groups A–H).

Typical for all forms of *C. javensis* is a stem diameter of 2–6 mm without leaf sheaths and to 10 mm with sheaths; internodes up to 30 cm long (usually shorter); a distinct ocrea, deep crimson when young; pinnate, ecirrate leaves to 40 cm long, flabellate terminal leaflets and the lowermost pair often swept back across the stem; a flagellum

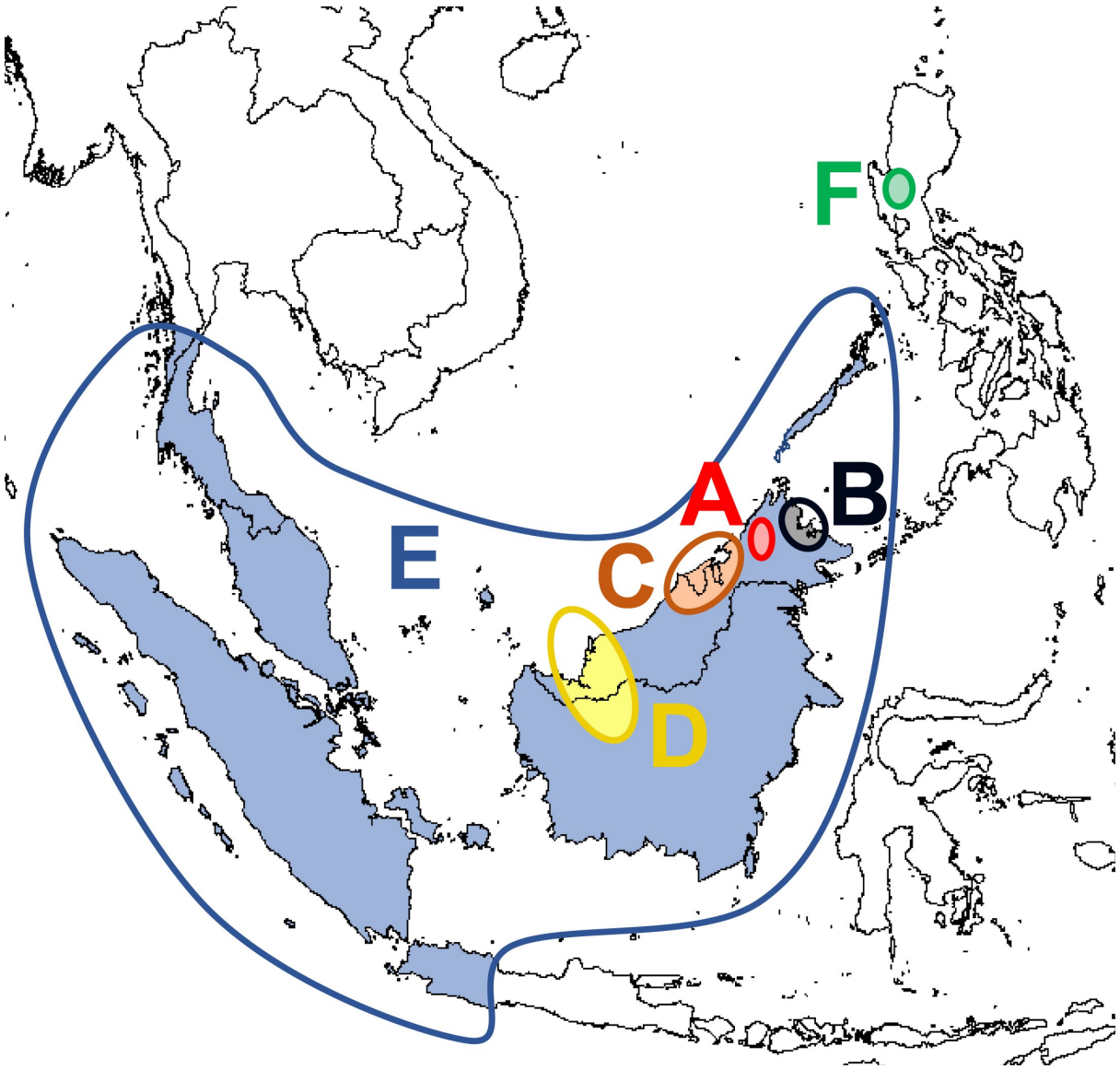

Fig. 1. Areas as used in the historical biogeographic analysis. A = NW Sabah (Borneo). B = NE Sabah (Borneo). C = Brunei with small parts of N Sarawak and SE Sabah (Borneo). D = central part of Sarawak and part of Kalimantan Barat (Borneo). E = remaining area, surrounding many of the former ones (S Thailand/S Myanmar up to Java and rest of Borneo). F = Central Luzon (Philippines).

to 75 cm long, long inflorescences with red rachillae and ripe fruits ovoid in shape. *Calamus tenompokensis* can be distinguished from the *C. javensis* complex by its short stem, angular petiole and rachis, a very different leaf sheath appearance (the sheaths being massive and robust), number (9 pairs) and almost always regularly arrangement of the leaflets, staminate calyx swollen (versus not swollen in *C. javensis*), pistillate inflorescences with rachilla bracts with a broadly cupuliform limb (versus bracts tightly sheathing in *C. javensis*).

One other form is phenetically and phylogenetically rather distinct, '*acuminatus*' (to be united with form '*polyphyllus*'); will be recognized as a variety of *C. javensis* (Atria *et al.*, ms., to be submitted, see there for justification). This taxon always has many (9–12) narrow or linear leaflets, subequidistant to regularly arranged, subopposite and with a smooth or almost smooth leaf sheath. The inflorescences resemble those of form *javensis*, but those are mostly smaller or finer. The size of flowers and fruits is smaller, and the bracts of the peduncle are more cupuliform than form *javensis*.

The biogeographical range of the *C. javensis* complex includes southern Thailand, the Malay Peninsula, Sumatra, West Java, Borneo and Luzon in the Philippines (Fig. 1). The greatest morphological diversity is found in north Borneo. The aim of this study is to see if historical

Table 1. Distribution area (Fig. 1) of the samples used in the phylogenetic analysis (Atria *et al.,* 2020). The group names (column 1) refer to mainly informal groups within *C. javensis* except for *C. tenompokensis* (recognized as species) and *acuminatus* (to be recognized as variety *polyphyllus* within *C. javensis*). All vouchers are in L (Naturalis Biodiversity Center, Leiden, the Netherlands) except *SAN 21064* in K (Royal Botanic Gardens Kew, UK).

Group name	Reference to molecular sample	Area	Voucher	Location
acuminatus	10A	B	*Mega MAT 037*	Sabah
acuminatus	10B	B	*Mega MAT 028*	Sabah
acuminatus	10C	C	*SAN 85869*	Sabah
acuminatus	10D	C	*SAN 126575*	Sabah
acuminatus	10E	B	*Mega MAT 033*	Sabah
acuminatus	6G	C	*Dransfield JD 5584*	Sabah
amplijugus	1E	C	*Mega MAT 109*	Brunei
amplijugus	3D	B	*Mega MAT 045*	Sabah
amplijugus	3F	C	*Mega MAT 109C*	Brunei
congestiflorus	12E	C	*Mega MAT 079*	Sabah
corrugatus	6C	D	*Dransfield JD 6080*	Sarawak
corrugatus	6E	D	*Mogea 3615*	Central Kalimantan
corrugatus	6F	D	*Dransfield JD 5868*	Sarawak
elopurensis	10F	B	*Dransfield JD 6265*	Sabah
Form2	8E	F	*Madulid et al. 7172*	Luzon
Form4	11G	B	*Chew & Corner RSNB 4835*	Sabah
Form4	12D	A	*Mega MAT 065*	Sabah
impar	11A	E	*Ave 136*	Malay Peninsula
impar	11B	E	*Niyomdham 1254*	S. Thailand
impar	11D	A	*SAN 21064*	Sabah
javensis	1A	E	*Mega MAT 001*	W. Java
javensis	1B	C	*Mega MAT 093*	Brunei
javensis	1C	E	*Mega MAT 022*	W. Java
javensis	1D	E	*Mega MAT 008*	W. Java
javensis	1F	E	*Mega MAT 011*	W. Java
javensis	1G	E	*Mega MAT 005*	W. Java
javensis	2C	C	*Mega MAT 100B*	Brunei
javensis	2E	E	*Mega MAT 024*	W. Java
javensis	3G	E	*Mega MAT 007*	W. Java
javensis	3H	E	*Mega MAT 002*	W. Java
javensis	4A	E	*Ave 114*	Malay Peninsula
javensis	4B	D	*Dransfield JD 4728*	Sarawak
javensis	4C	E	*Ambri & Arifin W 915*	E. Kalimantan
javensis	4D	E	*Kato & Wiriadinata B 4943*	E. Kalimantan
javensis	4H	D	*Dransfield JD 4650*	Sarawak
javensis	5A	E	*Dransfield JD 4519*	Malay Peninsula
javensis	5B	C	*S 50593*	Sarawak
javensis	5E	E	*Dransfield JD 3613*	Sumatra
javensis	6A	D	*S 54137*	Sarawak
javensis	6B	E	*van Valkenbrg 1320*	E. Kalimantan
javensis	7A	E	*Mega MAT 097*	Brunei
javensis	7C	C	*S 52424*	Sarawak
javensis	7F	E	*Dransfield JD 2553*	Sumatra
javensis	8B	E	*Mega MAT 057*	Sabah
javensis	8D	E	*Ave 216*	Malay Peninsula
polyphyllus	2B	C	*Mega MAT 103A*	Brunei
polyphyllus	3C	A	*Mega MAT 058*	Sabah
polyphyllus	10G	B	*Mega MAT 027*	Sabah
polyphyllus	12B	C	*Mega MAT 095*	Brunei
polyphyllus	12C	E	*Mega MAT 080*	Sabah
tenompokensis	10H	A	*Mega MAT 055*	Sabah
tenompokensis	11E	A	*Mega MAT 054*	Sabah

geographic patterns developed in the various forms.

MATERIALS AND METHODS

The results of the phylogenetic analysis (Fig. 2; Atria *et al.*, 2020) formed the basis for the historical biogeographic analysis. At first we opted for a phylogeographic analysis, as this provides better methodology for intraspecific relationships, but the signal in the molecular data was too weak. Therefore, only a simple historical biogeography analysis was the only alternative left. A total of 52 samples was used to sequence the nuclear 5S spacer and the chloroplast *mat*K regions. All samples, molecular methodology and phylogenetic methods are explained in Atria *et al.* (2020). *Calamus flabellatus* Becc. (silica sample) acted as outgroup in the phylogenetic parsimony and Bayesian phylogenetic analyses. The outgroup was removed again in the historical biogeography as it was unknown how closely related the *Calamus flabellatus* is to *C. javensis*.

Taxon sampling

The 52 samples of silica gel-dried leaf fragments and herbarium specimens comprised one of the syntypes, from west Java (*Blume* s.n. (L, sheet 900.182-94)), while also silica gel-dried material from the type locality was included. All samples cover the distribution area of the *C. javensis* complex. A list of voucher specimens can be found in Appendix 1 of Atria *et al.* (2020).

Areas

Areas are recognized via a combination of the distribution of informal groups (names in the phylogeny, Fig. 2; Atria *et al*., 2020) and supported monophyletic groups. The latter were very rare (indicated with letters A–H in Fig. 2) and, therefore, the specimens in all non-supported branches ended up in area E. The selection process resulted in the discrimination of the following areas (Fig. 1): A = NW Sabah (Borneo), B = NE Sabah (Borneo), C = Brunei with small parts of N Sarawak and SE Sabah (Borneo), D = central part of Sarawak and part of Kalimantan Barat (Borneo), E = remaining area, surrounding many of the former ones (S Thailand/S Myanmar up to Java and rest of Borneo), F = Central Luzon (Philippines). Table 1 shows the areas as per specimen.

Historical Biogeographic Analysis

All analyses were carried out in RASP v.4.0 (Reconstruct Ancestral State in Phylogenies; Yu *et al*., 2015). Three modules in RASP were used: parsimony-based S-DIVA (Statistical, DIspersal-VIcariance analysis; Ronquist, 1997), maximum likelihood based DEC (Dispersal Extinction Cladogenesis; Ree *et al*., 2005; Ree & Smith, 2008) and S-DEC (Statistical DEC). As input all cladograms (18,000, burn-in removed) found with a bayesian phylogeny analysis (Atria *et al*., 2020) were used and the Maximum Clade Credibility (MCC) tree derived from those cladograms. DEC only uses the MCC tree for the analysis, the Statistical modules reconcile all trees against the MCC tree, thus introducing a kind of consensus per branch in the MCC tree (and adding a more Bayesian approach to DIVA).

In all modules the number of areas allowed per node was increased from 2 to 6 (maximum possible) per analysis. All other settings were default, no additional time frames were added in DEC as the MCC tree (Atria *et al.*, 2020) was not dated.

RESULTS

The results of all analyses are summarized in Fig. 2 for the maximum number of areas (6) per node. Even though more areas were allowed, at most only 3 areas resulted as best optimisation per node, but usually 2 or a single area proved to be the best results. As could be expected, these optimisations, independent of the method, generally include area E as this is by far the largest surface and most specimens have this distribution. The areas mentioned per node (Fig. 2) are the ones with the highest probabilities, but as most node support was very low, therefore, these highest probabilities are also low and often many possible optimisations per node exist (not shown).

Even though most specimens occurred in area E, Borneo (areas A–D) is very important. In the upper clade (Fig. 2, nodes 54–67, containing the groups D–H) especially area B (NE Sabah), is important, followed by areas A (Kinabalu and adjacent areas) and C ("Brunei"). In the other clade (Fig. 2, nodes 68–103) these are especially areas C and D (central Sarawak, part of Kalimantan Barat) on Borneo. Of course area E comprises, among other areas, the rest of Borneo. No other obvious patterns were visible per form name or in most clades.

Of the groups that can be recognized it is obvious that *C. tenompokensis* (Fig. 2, group E) is only present in area A. The only other taxon is *C. javensis* var. *polyphyllus* (Fig. 2, mainly group F), which occurs in the Bornean areas B and C. Unfortunately, only represented once in the phylogeny, is 'Form 2', the only one found in in central Luzon, the Philippines (Fig. 2, halfway, blue).

DISCUSSION

The basal node (Fig. 2, node 104) indicates as best optimisation area BCE or BE, but these areas

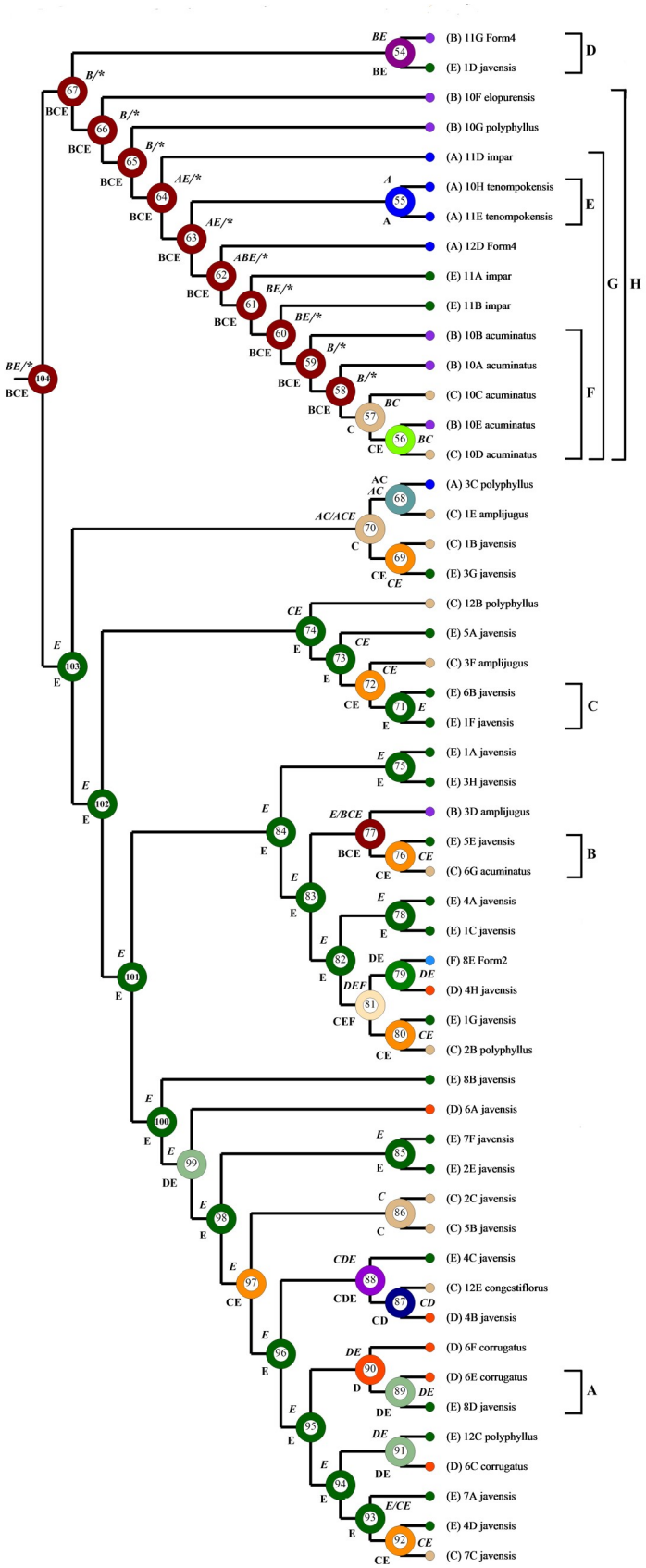

Fig. 2. Area cladogram for the *Calamus javensis* complex. The groups indicated are the ones with a high (0.85 posterior probability) in the phylogenetic analysis (Atria *et al.*, 2020). The terminal taxa have their distribution between brackets in front of the name. The various areas can be found in Fig. 1. On the internal nodes the optimisations according to S-DIVA (bold), DEC (bold italics) and S-DEC (if similar to DEC then only one value, otherwise behind the /).

cannot be regarded as the area of origin of *C. javensis*. For that purpose this phylogeny should be embedded in a much larger phylogeny, preferably the whole of *Calamus* (which has to include more markers than the phylogeny used here). Borneo is one of the oldest areas in W Malesia that was already (partly) above water more than 60 Ma (Hall, 2013), especially the southern part. This in combination with the high variability on Borneo may indicate that perhaps the species originated on Borneo, but at least it was already present on the island in an early phase of its evolution. The root node *Calamus* in Janssens *et al*. (2020) is *ca*. 60 Ma, when at least the southern part of Borneo was above water (Hall, 2013).

Of the three rainforest areas in the world Malesia differs from Amazonia and the Congo rainforest. During interglacial periods, like the present, the latter two occupy their largest surface area, while Malesia is then at its smallest (*e.g*., Morley & Flenley, 1987; Cannon *et al*., 2009). During glacial periods this reverses, drought reduces the rainforest areas in Amazonia and the Congo to refuge areas, while the forest in Malesia extends to its maximum due to the emergence of a dry Sunda Shelf (connecting the Malay Peninsula, Sumatra, Borneo and Java) and Sahul Shelf (connecting New Guinea to Australia). However, not the whole Sunda Shelf becomes an everwet area during glacial periods, a large savannah corridor (complete extend unknown: Cannon *et al*., 2009) develops from the Malay Peninsula via the lowest areas towards Java and involves the southern part of Borneo. NE Borneo (area B) often acts as a refuge area for species, as shown for the Dipterocarpaceae by Raes *et al.* (2014) via species distribution modelling for the last glacial maximum (21 kya). This might also have been an important refuge area for *Calamus javensis*, as area B is important in the upper clade (Fig. 2, nodes 54–67).

Calamus tenompokensis (group E in Fig. 2) is typically a local endemic that originated at the higher altitudes of Mount Kinabalu and the Crocker Range in NE Sabah (area A). Something similar applies to the '*acuminatus*' form (group F in Fig. 2), but the ecological conditions under which the form develops are less obvious. It occurs in areas B (NE Sabah) and C ("Brunei") and if the strongly resembling form '*polyphyllus*' is also included, then also once in area A (NW Sabah). All other forms (see names in Fig. 2) occur mixed throughout the phylogeny. This likely indicates that *C. javensis* is genetically and phenetically quite plastid, adapting (relatively quickly?) easily to varying environmental circumstances as long as these are in the more everwet areas, whereby similar forms can occur in very disjunct areas, that probably have a more or less similar habitat. This can be seen in Table 1 as various recognisable forms occur in different areas.

During glacial periods land bridges occurred, one ranges from NE Borneo via Mindanao to Luzon (*e.g*., Morley & Flenley, 1987: fig. 5.5). *Calamus javensis* may have dispersed to Luzon via this bridge, but as the climate and soils differed the species adapted, which resulted in 'Form 2'. Similar changes, can for instance also be seen in *Guioa pleuropteris* (Blume) Radlk. (Sapindaceae), where the leaflets became much smaller with a different hair type then found on Borneo (van Welzen, 1989: fig. 110). Similar geoclines, indicative of the landbridge, are also present in two other Sapindaceae: *Gloeocarpus patentivalvis* (Radlk.) Radlk. (van Welzen, 1991) and *Lepidopetalum perrottetii* (Cambess.) Blume (van Welzen *et al.*, 1992).

In conclusion, likely due to the lack of phylogenetic signal, it is obvious that the present analysis shows no historical biogeographic pattern behind the various recognisable forms in the *C. javensis* complex. Forms are very likely the result of adaptation to local circumstances, whereby more or less identical forms can develop under similar niche circumstances in disjunct areas. Exceptions are the '*acuminatus-polyphyllus*' form and *C. tenompokensis*, which are present in non-disjunct areas.

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